# Horizontal and vertical distribution patterns in

# *Macoma balthica*

## natural variation and the effect of manipulated densities

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# CONTENTS

# ABSTRACT

The patchy nature of environments combined with the behaviour of species determines the spatial arrangement of individuals. This spatial heterogeneity is functional within ecosystems and spatial structuring is therefore an important component of ecosystems. In this study the spatial distribution of *Macoma balthica* was determined in the field and combined with two density experiments on the spatial arrangement of individuals.

The spatial distribution and abundance of *Macoma balthica* was studied for two lengthclasses at an intertidal area of Richel in the western Wadden Sea. The depth distribution observed in the field displays a U-shaped relation with length. The preferred size class ($\leq$ 18 mm) for Knots, the main predator of *Macoma balthica*, was buried deepest. Macoma's $\geq$ 12.5 mm were found to exhibit a contagious distribution on a scale of 6 to 1100 metre radius. This in contrast to Macoma's < 12.5 mm, which showed a random distribution with a slight tendency towards a contagious distribution. The differences in distribution between the two length-classes might be attributed to a strategy of timely shifts during the first year of their lives. Dry and wet habitat sampled cores only showed a difference (not significant) in density at the largest sample size investigated.

In the field experiment on Richel there was a strong trend that density influenced depth distribution of *Macoma balthica* $\geq$ 12.5 mm. The factors length, $AFDM_{siphon}$, $DM_{shell}$ and $AFDM_{meat}$ have an effect on the depth distribution in the field experiment on Richel. In the IBN experiment contagious distributed Macoma's were buried significantly shallower than regular distributed Macoma's, a phenomenon which might be explained by the occurrence of intraspecific competition over food or other favourable conditions. Risk of predation is influenced by the foraging strategy of the predator and may also contribute to this phenomenon. Furthermore a relation was found between burying depth and total horizontal movement, which negatively correlated with each other. With increasing density the total horizontal movement increased significantly.

# INTRODUCTION

The study of spatial patterns is interesting from a fundamental point of view since it is an important population parameter especially in the study of predator-prey interactions (Meire et al., 1989). The spatial relation between the level of predation and resource density has important consequences regarding the dynamics and stability of plant and prey populations (Crawley, 1983; Hassel et al., 1987; Hassel et al., 1991; Rohani et al., 1994). Rate maximising consumers may be expected to aggregate in patches with higher density of resources, as found in many field studies (Curio, 1976; Hassell, 1978). Indeed stability of both, predator and prey populations, usually increases when the distribution of the prey population is more aggregated (Hassel, 1981).

Variation (patchiness) in the distribution of organisms and other environmental variables exist at different spatial scales. The environment is primarily structured by large scale (both spatial and temporal) abiotic factors, which define broad patterns of distribution (Barry and Dayton, 1991; Allen and Star, 1982). Within these patterns, other processes continually operate at smaller temporal and spatial scales to modify distribution and abundance's. These factors may be biotic (processes as reproduction, death, predator-prey interactions, food availability, parasitism and so on), abiotic or involve interactions between these two (Thrush, 1991). Spatial heterogeneity occurs as populations undergo spatial structuring through these processes (Allen and Star, 1982). Therefore spatial heterogeneity is functional within ecosystems and spatial structuring is an important component in ecosystems (Legendre, 1993).

The spatial pattern of a population is the result of two opposite ecological forces. First there is the search for maximum living space which results in a dispersion. On the other hand there is a tendency to aggregate as all similar organisms share the search for the best environmental conditions (Meire et al., 1989).

Characterisation of populations in space requires the definition of both intensity (density) and form of spatial patterns. Patterns can be classified into three groups: uniform, contagious (aggregated) and random (figure 1).
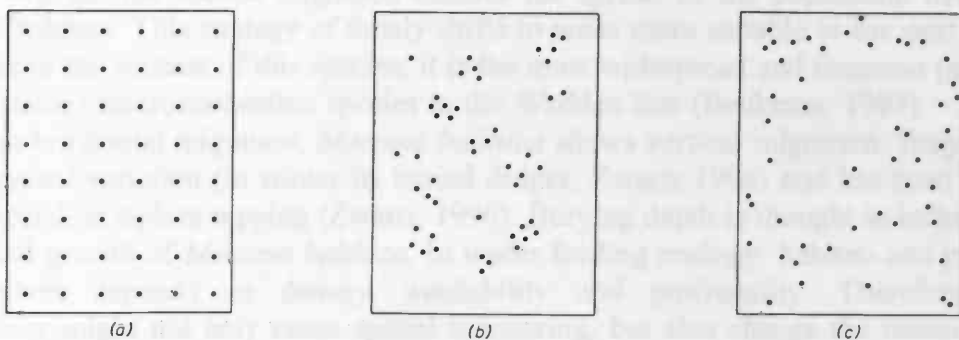


Figure 1.  Three different distribution patterns with the same density in two-dimensional space: a) uniform, b) contagious, c) random (from Zar, 1984)

4

The uniform pattern, resulting from intraspecific competition, often occurs in dense populations (Holme, 1950). The contagious or aggregated pattern can be explained by the heterogeneity of the environment, predation pressure, competition or reproductive behaviour (Meire *et al.*, 1989). Within these aggregated patterns usually there will be a regular distribution. Generally spoken: observed distribution of individuals over an area is (almost always) dependent on the scale of the study (van der Aart, 1985). Randomness only occurs when the density is so low that one studied individual has no member of the same species with which to respond. In contrast to dispersion in the abiotic world, the dispersive processes of living organisms involve intrinsic behavioural responses that make spatial randomness highly improbable. Nevertheless, randomness is often taken as a starting point to define spatial distributions in ecology because randomness and evenness are the only conditions which can be unequivocally defined (Taylor *et al.*, 1978).

In their study about the density dependence of spatial behaviour and the rarity of randomness, Taylor *et al.* concluded that spatial disposition is density-dependent and they deduced that spatial behaviour is also density-dependent.

In the marine environment, one of the most studied populations is *Macoma balthica*.

*Macoma balthica* is a common tellinid bivalve that lives buried in marine soft sediment of the northern boreal regions. This mollusc is an important prey for waders; e.g. Oystercatcher, *Haematopus ostralegus* (Hulscher, 1973; Zwarts, 1996) and Knot, *Calidris canutus* (Piersma, 1994; Zwarts, 1996). In the Wadden Sea it occurs at relatively high densities (tens or hundreds per $m^2$) at nearly all tidal flats (Beukema, 1976; Dankers and Beukema, 1983) and subtidal areas (Dekker, 1989).

It is a facultative suspension/deposit feeder, grows slowly (maximum length $\pm$ 27 mm) and diverts its resources into relative early reproduction at a length of $\pm$ 10 mm (Commito, 1982). *Macoma balthica* has a short synchronised spawning period in spring (Lammens, 1967; de Wilde, 1975) and the larval stage is pelagic.

During their first year in the Wadden Sea, high proportions of the tidal-flat populations of *Macoma balthica* redistribute twice in search of good conditions for survival. In summer the spat moves in shoreward direction and in winter grown spat with a length of about 5 mm, moves to the midtidal or lowtidal flats or further. The first move results in recruitment stability, whereas the second migration ensures the spread of the population over a wide variety of habitats. This strategy of timely shifts to areas more suitable to the next life stage contributes to the success of this species; it is the most widespread and common (and one of the most stable) macrozoobenthic species in the Wadden Sea (Beukema, 1993).

Apart from horizontal migration, *Macoma balthica* shows vertical migration. Burying depth shows seasonal variation (in winter its buried deeper, Zwarts 1996) and has been shown to further depend on siphon nipping (Zwarts, 1996). Burying depth is thought to influence both survival and growth of *Macoma balthica*. In wader feeding ecology, habitat- and preychoice among others depends on density, availability and profitability. Therefore, spatial heterogeneity might not only cause spatial structuring, but also change the outcome of the trade-off between safety and foraging. Thus variation in density could lead to differences in depth distribution, which of course affects the interaction between prey and predator.

The aim of this study was to investigate the spatial pattern (distribution pattern in space not depth) of *Macoma balthica* in the field at varying scales. In two experiments we studied at individual scale whether density and experimental distribution influenced the subsequent spatial and depth distribution.

5

## MATERIAL AND METHODS

### Fieldwork

Sampling was carried out on 9 May - 20 May 1997 on 4 different sites on Richel (figure 2). Richel is a low-lying barren sandflat in the western Wadden Sea covering 2.4 km².
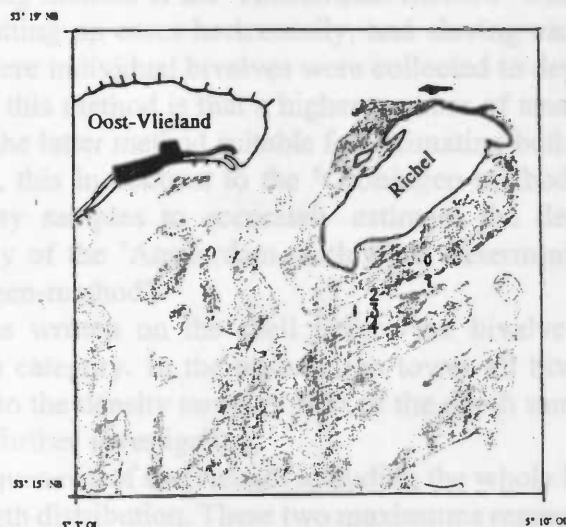


Figure 2. An overview of the study area Richel. The intertidal area indicated by shading and is bordered by the mean low water mark at spring lows (O = observation tower, 1=site 1, 2=site 2, 3=site 3, 4=site 4).

At each site a number of measurements were done, sampling density and depth. A round coring device with a diameter of 15 cm was pushed ± 20 - 25 cm into the sediment. Since the measurements were done as part of a predator exclosure program interactions, the sample sites were divided in exclosure/non-exclosure. An analysis of variance (ANOVA) showed that the distributions in length and depth of *Macoma balthica* did not differ significantly between exclosure, non-exclosure (depth: $R^2 = 0.01$; $F_{1,196} = 1.36$; $p = 0.25$, for length: $R^2 = 0.00$; $F_{1,966} = 0.15$; $p = 0.70$). In further analysis of the fielddata, all data of each site was combined, so there is only a division in sites and not within sites.

The cores for density sampling were sieved with a 1 mm mesh sieve. All Macoma's were put in a separate identifiable plastic bag. Afterwards they were counted and measured. Bivalve maximum length and minimum width was measured to the nearest 0.05 mm with vernier callipers (figure 3).
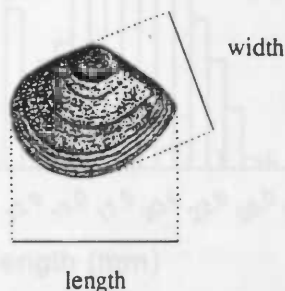


Figure 3. Measurements of the maximum length and the minimum width of *Macoma balthica*.

The depth distribution was assessed using two different methods; the 'Groningen-method' and the 'Amsterdam-method'. At each site both methods were performed simultaneously, both utilising core sampling. Using the 'Groningen-method', the depth of the bivalve was determined by cutting up cores in thin vertical slices until a bivalve was encountered. The distance between the upper edge of the shell and the surface was measured. Individual bivalves were assigned to depth categories of 0.5 cm above a depth of 5 cm, and on 1 cm below 5 cm depth.

A more time consuming method is the 'Amsterdam-method' where the depth of the bivalve was determined by cutting up cores horizontally, and sieving each cm of the sediment over a 1 mm mesh sieve. Here individual bivalves were collected to depth categories to the nearest cm. The advantage of this method is that a higher number of small bivalves (ca. 10 mm) are detected. This makes the latter method suitable for estimating both density and depth distribution at the same time, this in contrast to the 'Groningen-method' where the data has to be combined with density samples to accurately estimate the depth-density distribution of bivalves. The accuracy of the 'Amsterdam-method' in determining bivalve depth might be less than the 'Groningen-method'.

The core number was written on the shell before the bivalve was put in a plastic box representing his depth category. In the observation tower all bivalves were sorted, counted and measured similar to the density samples. Part of the depth samples were frozen and taken to the laboratory for further investigation.

Figure 4 depicting frequencies of shell length including the whole Macoma field dataset shows two maximums in length distribution. These two maximums represent the different yearclasses in the population of *Macoma balthica*. There is a minimum between the first and the older yearclasses at a shell length of 12.5 mm. In this study the population of *Macoma balthica* was devided in two lengthclasses for further analysis: whether *Macoma balthica* < 12.5 mm (young) have a different distribution than Macoma balthica ≥ 12.5 mm (old).
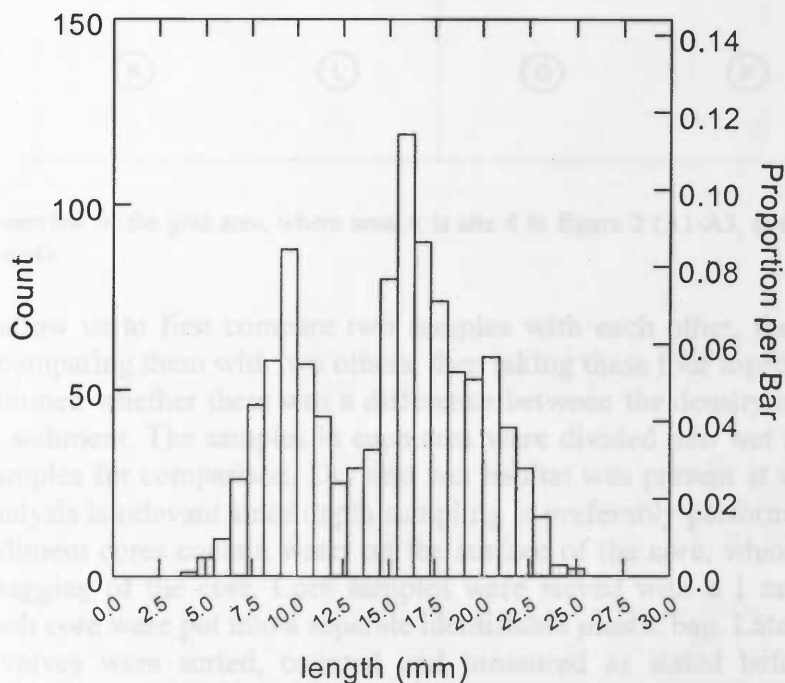


Figure 4. Size-frequency distribution of *Macoma balthica* from all sites on Richel, May 1997.

The density and depth samples of the 'Amsterdam-method' were used for spatial distribution analysis. For each core individual Macoma's divided in two length classes were counted. The frequencies of counts per core of each site were determined so the mean density (counts per core) and the variance could be calculated.

**Grid**

At 20 May 1997 a grid was density sampled. Every 28 metre a number of samples was taken from a small area, but the number of samples differed per area (figure 5).
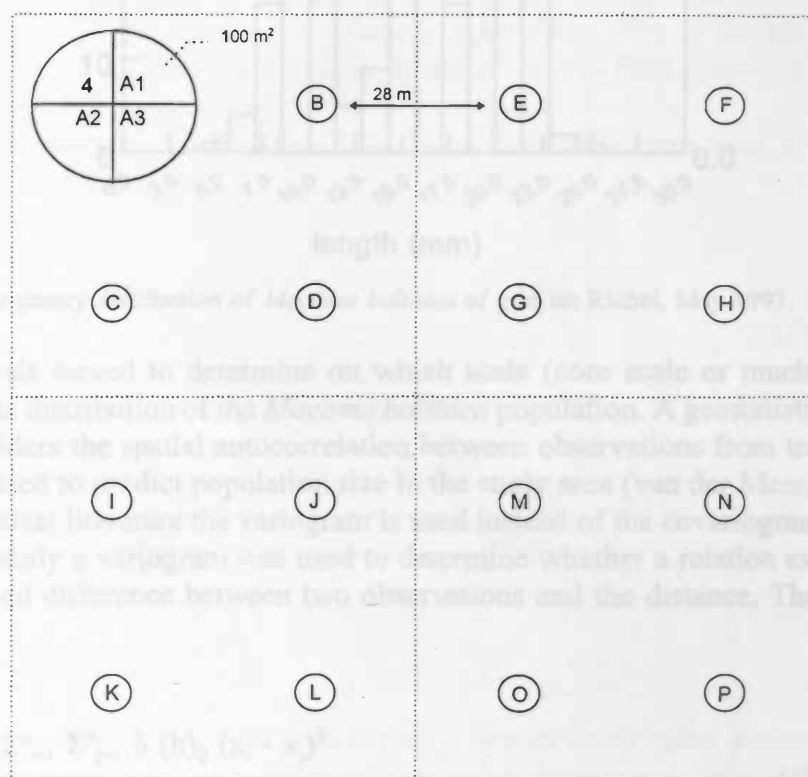


Figure 5. An overview of the grid area, where area A is site 4 in figure 2 (A1-A3, n=6; A4, n=30; B-D, n=8; E-P, n=4).

This was to allow us to first compare two samples with each other, then taking these two together and comparing them with two others, then taking these four together etc. Within each area we determined whether there was a difference between the density of *Macoma balthica* in wet or dry sediment. The samples in each area were divided into wet habitat samples and dry habitat samples for comparison. Dry and wet habitat was present at very small scales (< 5 m). This analysis is relevant since depth sampling is preferably performed on dry sediment cores: wet sediment cores contain water on the surface of the core, which leads to sediment run off and sagging of the core. Core samples were sieved with a 1 mm mesh sieve. The bivalves of each core were put into a separate identifiable plastic bag. Later in the observation tower the bivalves were sorted, counted and measured as stated before. For each core (different areas) the individual Macoma's were scored for two length classes. These data showed a comparable distribution of length as found in the fielddata (figure 6).
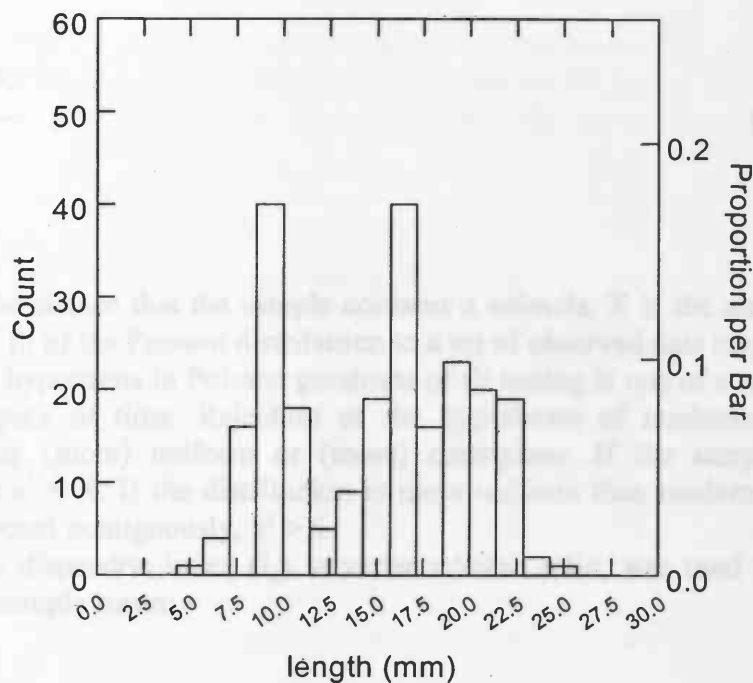
8

Figure 6. Size-frequency distribution of *Macoma balthica* of grid on Richel, May 1997.

The grid analysis served to determine on which scale (core scale or much larger) there is patchiness in the distribution of the *Macoma balthica* population. A geostatistical model which explicitly considers the spatial autocorrelation between observations from transect segments, was therefore used to predict population size in the study area (van der Meer, 1997). In much of the geostatistical literature the variogram is used instead of the covariogram (van der Meer, 1997). In this study a variogram was used to determine whether a relation exists between the expected squared difference between two observations and the distance. The variogram was estimated by:

$$2 \gamma (h) = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} \delta (h)_{ij} (x_i - x_j)^2}{\sum_{i=1}^{n} \sum_{j=1}^{n} \delta (h)_{ij}} \tag{1}$$

where h is the distance between i and j, $x_i$ is the observed value at area i, and $x_j$ is the observed value at area j and $\delta(h)_{ij}$ is one (van der Meer, 1997).

In the following analysis frequencies determined during fieldwork and in the grid were both used. The accuracy with which *Macoma balthica* densities are described by our sampling regime depends on the spatial pattern of the *Macoma balthica* and both can be summarised in plots of variance on mean density (e.g. Beukema et al 1983).

Random distribution was taken as a starting point for attempts to define spatial distribution. The Poisson distribution is important in describing random occurrences, this occurrences being either objects in space or events in time. So here the expected frequency distribution will be a Poisson distribution:

9

$$P(x) = \frac{e^{-X} \cdot X^x}{x!} \qquad (2)$$

Where $P(x)$ is the chance that the sample contains x animals, X is the sample mean.
The goodness of fit of the Poisson distribution to a set of observed data may be tested by Chi-square. The null hypothesis in Poisson goodness of fit testing is one of a random distribution of entities in space or time. Rejection of the hypotheses of randomness results in the distribution being (more) uniform or (more) contagious. If the sample has a random distribution than $s^2 = X$. If the distribution is more uniform than random $s^2 < X$ and if the sample is distributed contiguously, $s^2 > X$.
In this study the dispersion index ($I_d$), a variance/mean ratio, was used for analysing randomness of the sample mean;

$$I_d = \frac{VAR\,(n-1)}{X} \qquad (3)$$

(Zwarts, 1988).
When $I_d$ is one the distribution is random ($Id = 1$) for an $I_d < 1$, the distribution is uniform and for an $I_d > 1$, the distribution is contagious.

## Field experiment Richel

From 16 May 1997 to 19 May 1997, on Richel a density experiment was carried out to test whether different densities of *Macoma balthica* cause different individual behaviour. Other factors, like siphon weight, shell length, sex and so on, which may have a relationship with the burying depth (vertical distribution) were also analysed. In this experiment migration caused by differences in density was the main interest.
A quadrant of 2 by 2 metres was digged, about 20 cm deep. The contours of the quadrant were bordered with long strips of plastic to a depth of 30 cm to prevent (im)migration. All digged up sand was sieved back into the quadrant over an 1 mm mesh sieve, thus removing all animals larger then this.
After one high tide a grid was created with wooden sticks and a cord (figure 7).The 25 plots were 25 x 25 cm plus a border of 5 cm, so the area marked with the cord is 35 x 35 cm. The cord prevented predators like Knots and other waders could disturb the experiment. However, there was no protection against other possible predators like crabs.
Macoma's were collected in the neighbourhood of site 2,3,4 (figure 2). The Macoma's were selected on length (> 15 mm). The density for each plot was randomly fixed. At the same time the Macoma's were numbered with a permanent marker, each number corresponding with the plot number. Densities were chosen in relation to data collected in the field (site 1 ± 80 Macoma's per m², site 2,3,4 ± 120 Macoma's per m²): 60 Macoma's per m² (low

density), 120 Macoma's per m$^2$ (density estimation of site 2,3,4), 480 Macoma's per m$^2$ ( 4 times higher than observed in the field) and 1920 Macoma's per m$^2$ (16 times higher than observed in the field). The number of plots decreased with increasing density.

| | | | | |
|---|---|---|---|---|
| 64 | 64 | 128 | 128 | 64 |
| 64 | 1920 | 64 | 64 | 128 |
| | 480 | 480 | 480 | 64 |
| 64 | 480 | 64 | 64 | 128 |
| 64 | 1920 | 128 | 128 | 64 |

Figure 7. An overview of the experiment Richel on the intertidal area (see figure 2). The numbers in each plot (area plus border is 35 x 35 cm) corresponds with the density of Macoma per m$^2$ and were randomly fixed (64/m$^2$, n=12; 128/m$^2$, n=6; 480/m$^2$, n=4; 1920/m$^2$, n=2).

After creating the grid, in each plot the bivalves were put into the sediment with the end of the siphon up (figure 8).
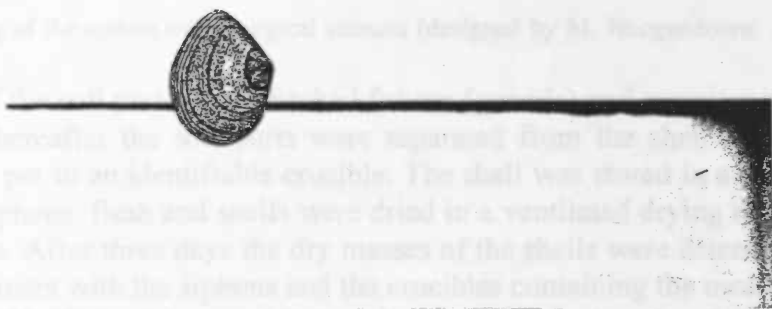


Figure 8. Situation of *Macoma balthica* at the start of the experiment.

After five times high tide, two cores were taken of each plot for density sampling. The 'Groningen-method' was used since the distance between the upper edge of the shell and the sedimentsurface could be measured up to mm accurately. The Macoma's were divided in the same categories as the 'Groningen-method' in the field except that the mm exact of its depth

11

was noted on the shell with a permanent marker. Plotnumbers and shellnumbers of the Macoma's were checked. When both numbers did not correspond, the number of the plot the Macoma was found in was also written on the shell. All depth sampled Macoma's were frozen and stored at -20 °C (21 May 1997, Texel) for further analysis.

The remaining sediment of the plot plus the 5 cm border (35 x 35 cm) was digged out and sieved with a 1 mm mesh sieve. In each plot the recovered Macoma's were counted and checked on plot number.

In the laboratory, all Macoma's were counted and measured for length, width and height to the near 0.05 mm as described before and the yearrings on the shell were counted. Using a binocular microscope the contractor of the shell was cut using small surgical scissors.

The siphon of the inflow (restricting Macoma depth) was carefully dissected (figure 9) and placed individually in a small platinum container. Siphonweight has been used before as a measure of siphonsize (Reading and Mc. Grorty, 1978; Kamermans, 1992; Zwarts, 1996).
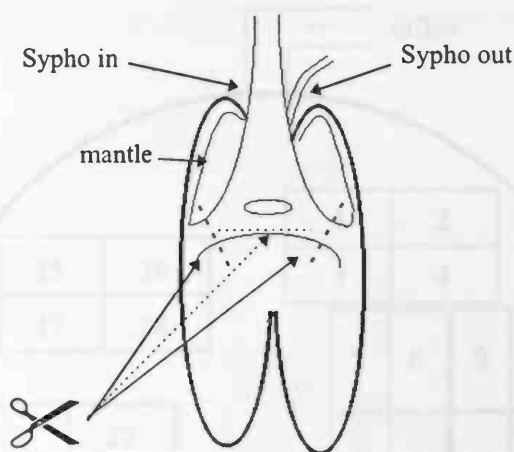


Figure 9. Cutting of the siphon using surgical scissors (designed by M. Hoogendoorn, 1997).

The remains of the soft parts were checked for sex (gonads) and parasites using the binocular microscope. Thereafter the soft parts were separated from the shell and the meat of each individual was put in an identifiable crucible. The shell was stored in a numbered hole of an eggbox. The siphons, flesh and shells were dried in a ventilated drying oven at 55 - 60 °C to a constant mass. After three days the dry masses of the shells were determined ($DM_{shell}$). The platinum containers with the siphons and the crucibles containing the meat were weighed and incinerated at 550 °C for 2 hours. After cooling in a dessicator, the platinum containers and the crucibles plus their content where reweighed. The difference between the first weighing and the second weighing is the ash-free dry mass ($AFDM_{siphon}$ and $AFDM_{meat}$). The balance used for siphon weighing was one decimal more accurate than the balance used for weighing the meat.

12

## Experiment IBN

During the period from 19 June 1997 to 31 July 1997 a second density experiment was carried out in a reservoir at the area of the Institute for Forestry and Nature Research (IBN, Texel). The effects of density and spatial distribution on movement (horizontal distribution) and burying depth (vertical distribution) was studied.

A tidal reservoir with an intersection of about 2 metres and a depth of about 1.25 metre was used for this experiment. Seawater was pumped from the Wadden Sea into a channel and into a serie of reservoirs, constantly refreshing the water even with low tide, which prevented extreme watertemperatures. The tide changed every 6 hours. The possibility of predation was absent.

Seven containers (60 x 40 x 30 cm) were put in the reservoir in such a way that when the tide was low in the reservoir the surface of the containers was exposed. Each container was divided into four plots with plastic (figure 10) and were filled with dried sandy sediment (sediment without benthic organisms) up to the rim of the container. After wetting of the sand the boxes were refilled up to the rim.
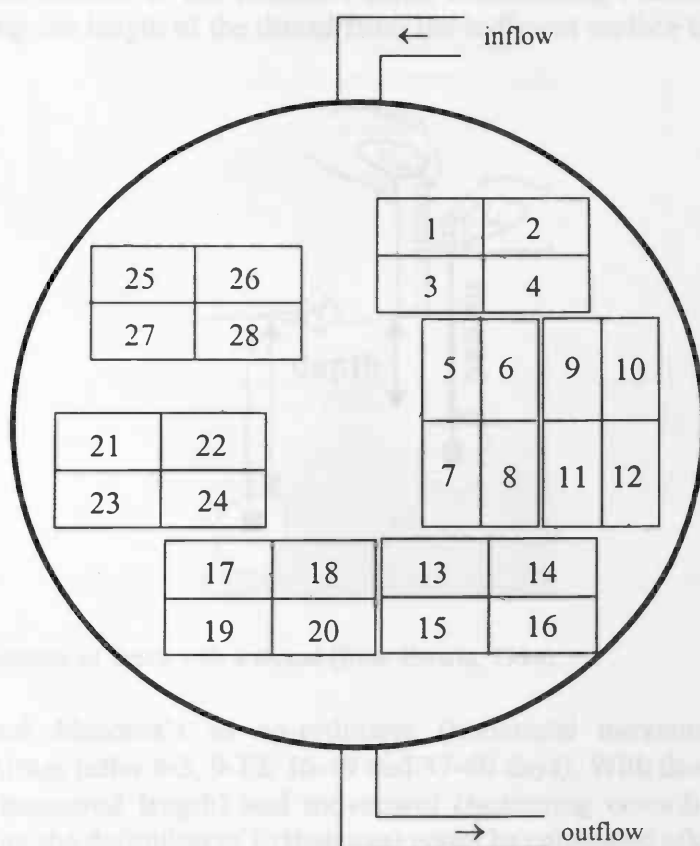


Figure 10. An overview of the experiment IBN.

Macoma's were collected on the tidal flats of 'de Schorren' on 18 June 1997. In the laboratory the shell length and shell width were measured with a digital vernier callipers to the near 0.01 mm. The surface of the shell was dried and a thin nylon thread with a identifiable label was attached to the shell using super glue and a little square of tape. The thread length was measured after it was glued on the shell.

13

The density and the spatial distribution of each plot was randomly fixed (table 1).

Table 1. An overview of the density and spatial distribution of each plot.

| plotnumber | density (#/plot) | density (#/m²) | distribution |
|---|---|---|---|
| 6; 22 | 50 | 965 | regular |
| 1; 28 | 50 | 965 | contagious |
| 10; 15; 16; 19 | 17 | 328 | regular |
| 9; 11; 17; 25 | 17 | 328 | contagious |
| 2; 5; 7; 13; 18; 20; 26; 27 | 4 | 77 | regular |
| 3; 4; 8; 12; 14; 21; 23; 24 | 4 | 77 | contagious |

The Macoma's were put into the sediment (figure 8) and the co-ordinates of every individual Macoma were determined with a ruler. All determinations of the co-ordinates used a similar standard point; the middle of the container (0,0). Determining Macoma burying depth was done by measuring the length of the thread from the sediment surface to the label (figure 11).
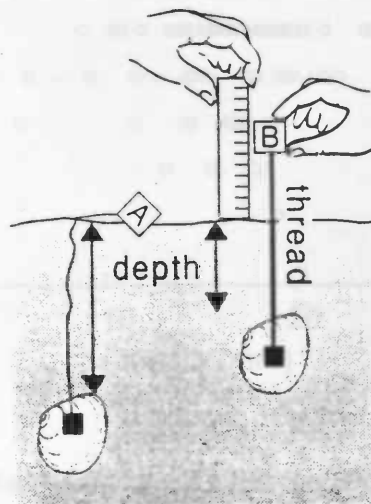


Figure 11. Measurements of depth with a thread (from Zwarts, 1996).

For all individual Macoma's its co-ordinates (horizontal movement) and depth were determined four times (after 4-5, 9-12, 16-19 and 37-40 days). With these data the depth (total thread length - measured length) and movement (beginning co-ordinates - measured co-ordinates and using the definition of Pythagoras) could be calculated after every measurement.

**Statistical Analysis**

Systat was used for all statistical analysis except the Chi-square analysis (Poisson distribution and the Binomial distribution). For these analyses Microsoft Excell was used. A significance level of 5% was used in all tests. Analysis with a stepwise General Linear Model (GLM) under Systat (1996) used a tolerance of 0.15 in determining the model best fitting the data.

14

## RESULTS

### Fieldwork

The depth distribution of *Macoma balthica* in the field showed an increase of depth with an increase of length until 15 mm shell length (figure 12). Macoma's with shell lengths between 15-18 mm were distributed around the same average depth. Macoma's larger than 18 mm showed a decrease.



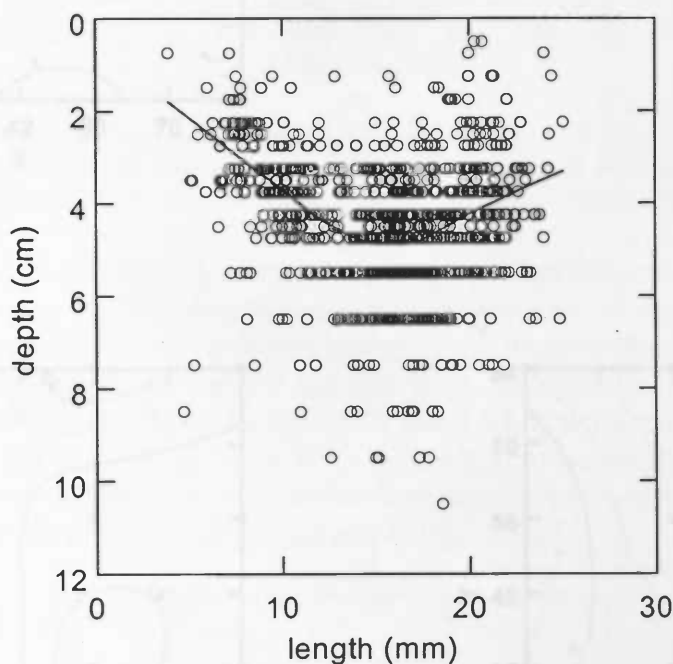Figure 12. The burying depth of *Macoma balthica* as a function of shell size, Richel 1997.

### Grid

Figure 13 shows an impression of the spatial distribution for recovered Macoma's and both length classes. The high density found at co-ordinates (56,28) in the overall distribution is caused by both lengthclasses. Macoma's of the lengthclass ≥ 12.5 mm caused the high density determined at (84,0). Area A4 (0,0) (with considerable more sampled cores), showed no remarkable difference in average density compared with the other plots. The distribution patterns show little difference within the whole grid and no aggregated distribution is evident.
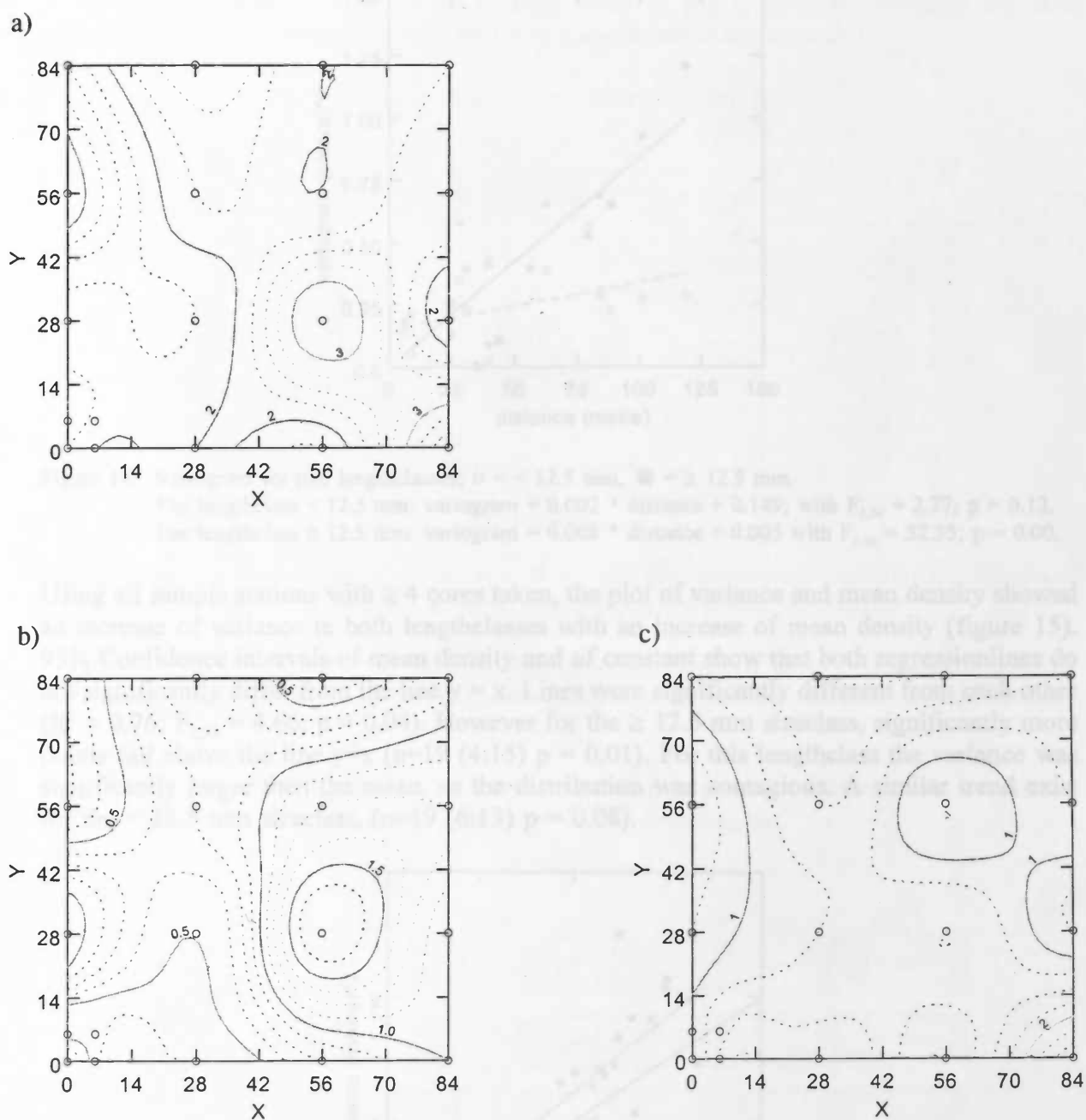
15

a)



b)



c)



Figure 13. Spatial distribution of *Macoma balthica* within the grid determined by density sampling, 20 May 1997, Richel: a) distribution of all recovered Macoma's; b) distribution of lengthclass < 12.5 mm; c) distribution of lengthclass ≥ 12.5 mm.

With increasing sampling distance there was an increase in variance in both lengthclasses (figure 14). The variogram for lengthclass ≥ 12.5 mm increased significantly with an increase in distance. There was no significant increase for lengthclass < 12.5 mm, which showed a random distribution with a slight tendency towards a contagious distribution.
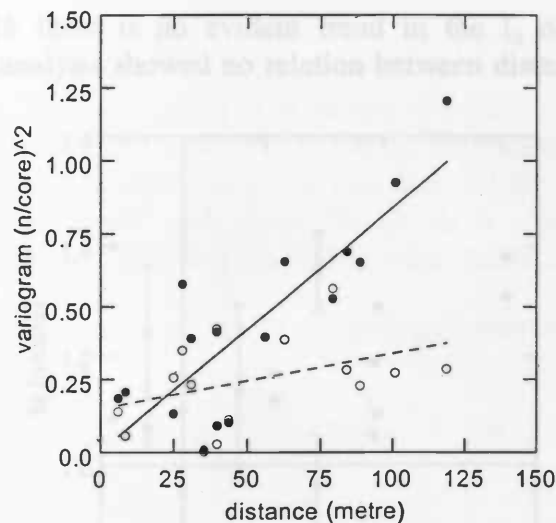
16

Figure 14. Variogram for two lengthclasses; o = < 12.5 mm, ● = ≥ 12.5 mm.
For lengthclass < 12.5 mm: variogram = 0.002 * distance + 0.149; with $F_{1,16}$ = 2.77; p = 0.12.
For lengthclass ≥ 12.5 mm: variogram = 0.008 * distance + 0.005 with $F_{1,16}$ = 32.35; p = 0.00.

Using all sample stations with ≥ 4 cores taken, the plot of variance and mean density showed an increase of variance in both lengthclasses with an increase of mean density (figure 15). 95% Confidence intervals of mean density and of constant show that both regressionlines do not significantly differ from the line y = x. Lines were significantly different from each other ($R^2$ = 0.76; $F_{1;38}$ = 4.66; p = 0.04). However for the ≥ 12.5 mm sizeclass, significantly more points fall above the line y=x (n=19 (4:15) p = 0.01). For this lengthclass the variance was significantly larger then the mean, so the distribution was contagious. A similar trend exist for the < 12.5 mm sizeclass, (n=19 (6:13) p = 0.08).
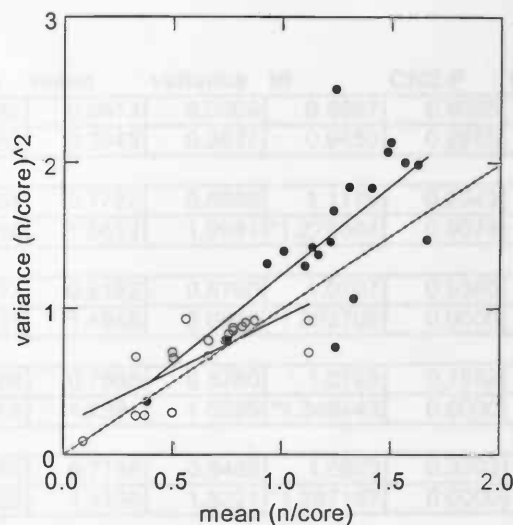


Figure 15. Variance and mean density plot for both lengthclasses; o < 12.5 mm, ● ≥ 12.5 mm. Line y = x (variance = mean) is the predicted line of a random distribution.
For lengthclass < 12.5 mm: variance = 0.73 * mean density + 0.21, with $R^2$=0.56; $F_{1;19}$=21.89; P=0.00; confidence interval of mean density 0.40 < 95% < 1.06 and of constant -0.02 < 95% < 0.44.
For lengthclass ≥ 12.5 mm: variance = 1.21 * mean density + 0.02, with $R^2$=0.05; $F_{1;19}$=17.24; P=0.00; confidence interval of mean density 0.60 < 95% < 1.83 and of constant -0.76 < 95% < 0.80.

17

As shown in figure 16 there is no evident trend in the $I_d$ over the distance for both lengthclasses. A GLM analysis showed no relation between distance and $I_d$.



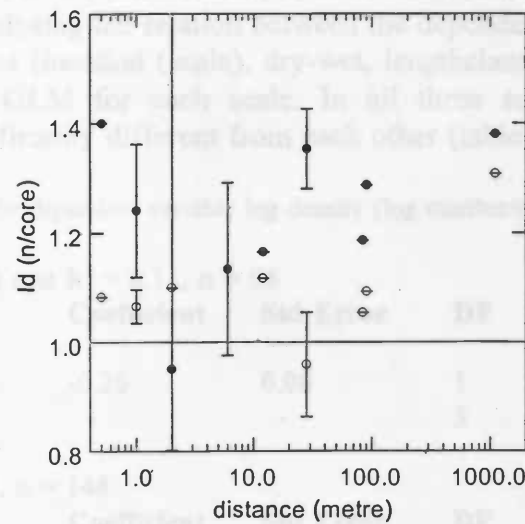Figure 16. For two lengthclasses; $\circ$ = < 12.5 mm, $\bullet$ = $\geq$ 12.5 mm, the dispersion index ($I_d$) as a function of the distance with line $I_d$ = 1 being the predicted line of a random distribution.

A large variation was observed between the mean densities of sample sites (table 2). The determined mean density and the expected mean density sometimes differed significantly (table 2).

Table 2. An overview of the different variables used in the analysis of the $I_d$ for different sites and area A4. Asterisk denotes $I_d$ significantly different (P =< 0.05) from random.

| place 1 | N cores | mean | variance | Id | Chi2 P | Chi2 | df |
|---|---|---|---|---|---|---|---|
| < 12.5 mm | 252 | 0.0913 | 0.0909 | 0.9957 | 0.9985 | 0.0317 | 3 |
| >= 12.5 mm | 252 | 0.3849 | 0.3637 | 0.9450 | 0.2955 | 4.9206 | 4 |
| place 2 | | | | | | | |
| < 12.5 mm | 184 | 0.7772 | 0.8688 | 1.1179 | 0.2049 | 8.4810 | 6 |
| >= 12.5 mm | 184 | 1.5652 | 1.9981 | *1.276564 | 0.0079 | 20.7166 | 8 |
| place 3 | | | | | | | |
| < 12.5 mm | 33 | 0.8182 | 0.8760 | 1.0707 | 0.9390 | 1.7768 | 6 |
| >= 12.5 mm | 33 | 1.4848 | 2.0680 | *1.392702 | 0.0000 | 44.1773 | 8 |
| place 4 | | | | | | | |
| < 12.5 mm | 168 | 0.7588 | 0.8280 | 1.0783 | 0.7532 | 3.4307 | 6 |
| >= 12.5 mm | 168 | 1.2381 | 1.6695 | *1.348443 | 0.0000 | 34.2793 | 7 |
| place 2,3,4 | | | | | | | |
| < 12.5 mm | 385 | 0.7766 | 0.8488 | 1.0929 | 0.3203 | 7.0062 | 6 |
| >= 12.5 mm | 385 | 1.4156 | 1.8221 | *1.287167 | 0.0000 | 35.5573 | 8 |
| place 1,2,3,4 | | | | | | | |
| < 12.5 mm | 637 | 0.5055 | 0.6613 | *1.308170 | 0.0000 | 41.2252 | 6 |
| >= 12.5 mm | 637 | 1.0078 | 1.3908 | *1.379954 | 0.0000 | 171.7808 | 8 |
| plot A4 | | | | | | | |
| < 12.5 mm | 30 | 0.8333 | 0.9023 | 1.0830 | 0.6420 | 4.2563 | 6 |
| >= 12.5 mm | 30 | 0.9333 | 1.3058 | 1.4000 | 0.2092 | 8.4155 | 6 |

## Dry-wet habitat

After log-transformation, data were divided in three scales from small to large; area A, areas A-D and areas A-P. Analysing the relation between the dependent variable, log-density, and the independent variables (location (scale), dry-wet, lengthclass and their interactions) was done with a stepwise GLM for each scale. In all three scales the densities of both lengthclasses were significantly different from each other (table 3).

table 3. Stepwise GLM of the dependent variable log density (log number/core) on different scale.

**Area A (A1, A2, A3, A4) met $R^2 = 0.11$, n = 96**

| Factor | Coefficient | Std Error | DF | F | 'p' |
|---|---|---|---|---|---|
| lengthclasses | -0.20 | 0.06 | 1 | 10.01 | 0.00 |
| lengthclasses*subplot | - | - | 3 | 2.01 | 0.12 |

**Areas A-D met $R^2 = 0.04$, n = 144**

| Factor | Coefficient | Std Error | DF | F | 'p' |
|---|---|---|---|---|---|
| lengthclasses | -0.10 | 0.04 | 1 | 6.25 | 0.01 |

**Areas A-P met $R^2 = 0.07$, n = 240**

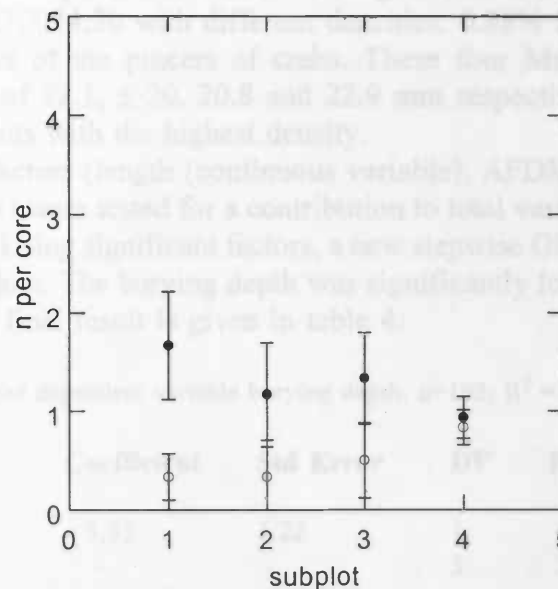| Factor | Coefficient | Std Error | DF | F | 'p' |
|---|---|---|---|---|---|
| dry-wet | 0.07 | 0.04 | 1 | 2.95 | 0.09 |
| lengthclasses | -0.11 | 0.03 | 1 | 11.22 | 0.00 |
| dry-wet*areas A-D | - | - | 3 | 1.81 | 0.15 |



Figure 17. Density (number/core) of *Macoma balthica* as a function of area A (A1, A2, A3, A4) at two lengthclasses, o = < 12.5 mm, ● = ≥ 12.5 mm ($R^2 = 0.11$; $F_{3,96} = 2.01$; p = 0.12).

Differences in density between dry-wet habitat was only found in the largest scale were the densities in the dry habitat were higher than densities in wet habitat. The categorical variable dry-wet and the interaction dry-wet * scale played an important role in the model, but were not significant (figure 18).
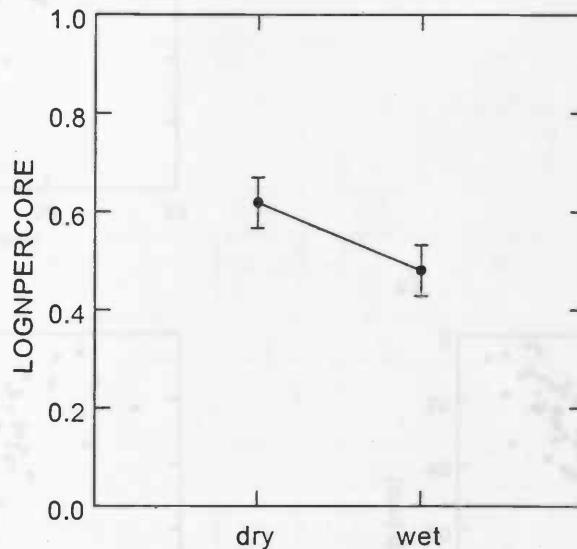


Figure 18. Density (log number/core) of *Macoma balthica* as a function of dry-wet habitat sampling for all areas combined ($R^2 = 0.07$; $F_{1;240} = 2.95$; $p = 0.09$).

## Field experiment Richel

At the end of the density experiment 93.6% of the Macoma were recovered, 92.5% was recovered in their original plot and 1.1% had migrated into another plot. These were Macoma's from plots 4;7;7;24;20 with different densities. 0.88% Macoma's died and were all recovered with marks of the pincers of crabs. These four Macoma's were from plots 22;22;7;1 with a length of 22.1, ± 20, 20.8 and 22.9 mm respectively. Three of these four Macoma's were from plots with the highest density.

In a stepwise GLM all factors (length (continuous variable), $AFDM_{meat}$, $AFDM_{siphon}$, $DM_{shell}$, density, parasites and sex) were tested for a contribution to total variance in depth (depth data was normal distributed). Using significant factors, a new stepwise GLM was created including interactions between factors. The burying depth was significantly lower with increasing shell lengths (figure 19). The final result is given in table 4.

Table 4. Stepwise GLM of the dependent variable burying depth; n=195; $R^2 = 0.49$.

| Factor | Coefficient | Std Error | DF | F | 'p' |
|---|---|---|---|---|---|
| length | - 3.52 | 1.22 | 1 | 8.39 | 0.00 |
| density | - | - | 3 | 2.50 | 0.06 |
| $AFDM_{siphon}$ | $1.42*10^4$ | $3.98*10^3$ | 1 | 12.80 | 0.00 |
| $DM_{shell}$ | -13.59 | 5.99 | 1 | 5.16 | 0.024 |
| length*$AFDM_{meat}$ | 10.76 | 3.24 | 1 | 11.01 | 0.001 |
| $AFDM_{siphon}*AFDM_{meat}$ | - $5.94*10^4$ | $2.83*10^3$ | 1 | 4.41 | 0.037 |

a)



b)

c)
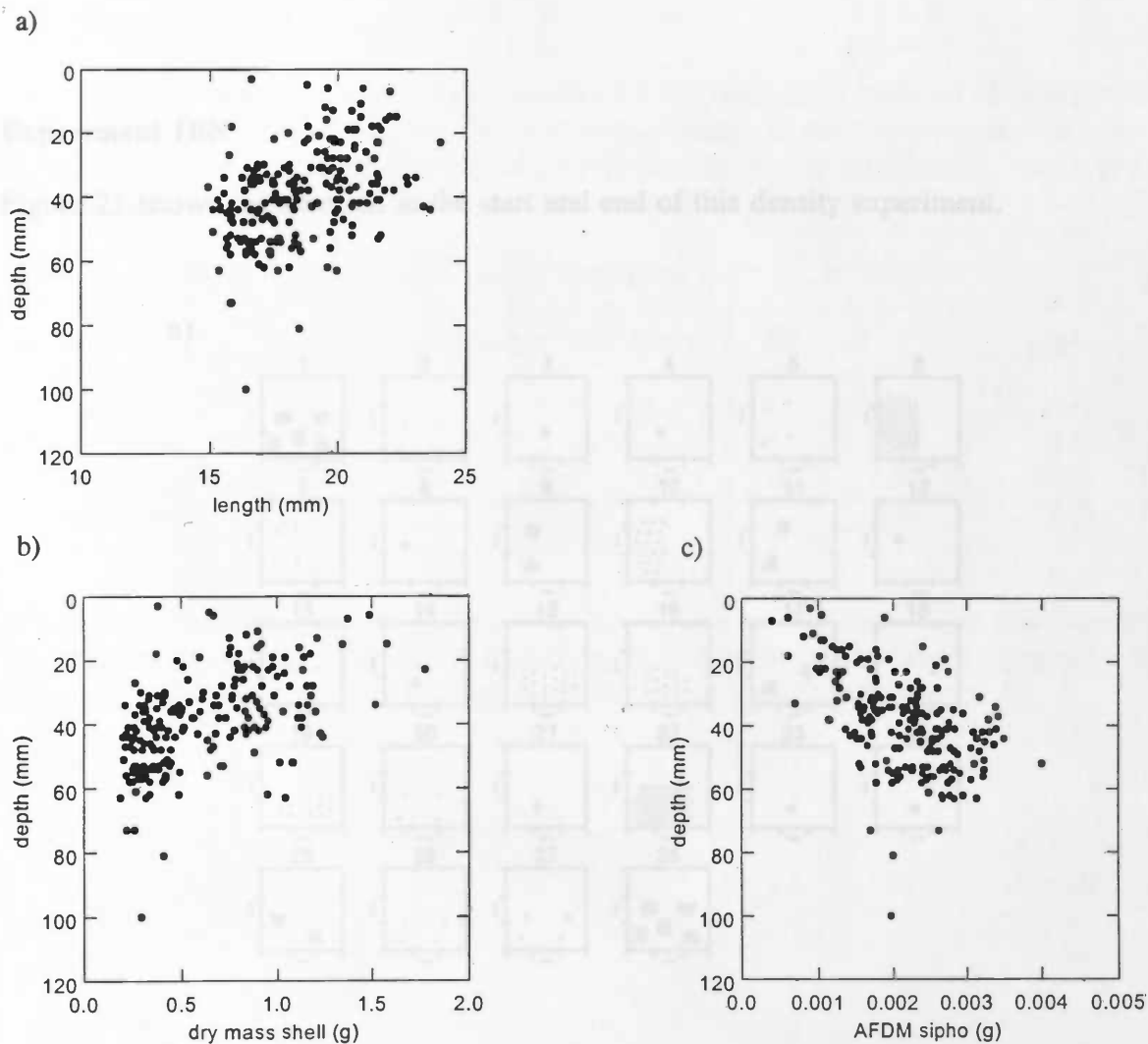


Figure 19. Burying depth of *Macoma balthica* as a function of, A : shell length, B : $DM_{shell}$, C : $AFDM_{siphon}$.

Significant changes with increasing densities were not observed, but density plays an important role in the model (figure 20). Densities of 64 and 1920 per square metre exhibit relatively deeper mean burying depths.
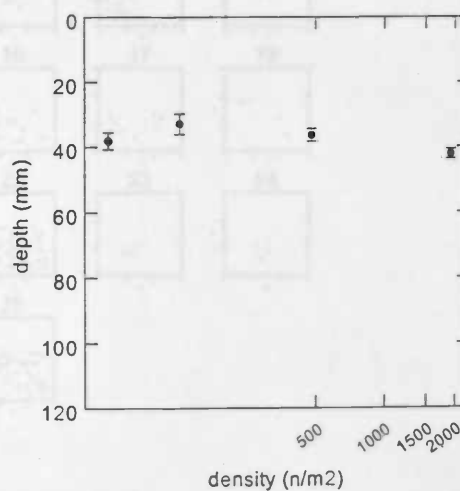


Figure 20. Burying depth of *Macoma balthica* as a function of the density (number/m$^2$).

21

**Experiment IBN**

Figure 21 shows the situation at the start and end of this density experiment.
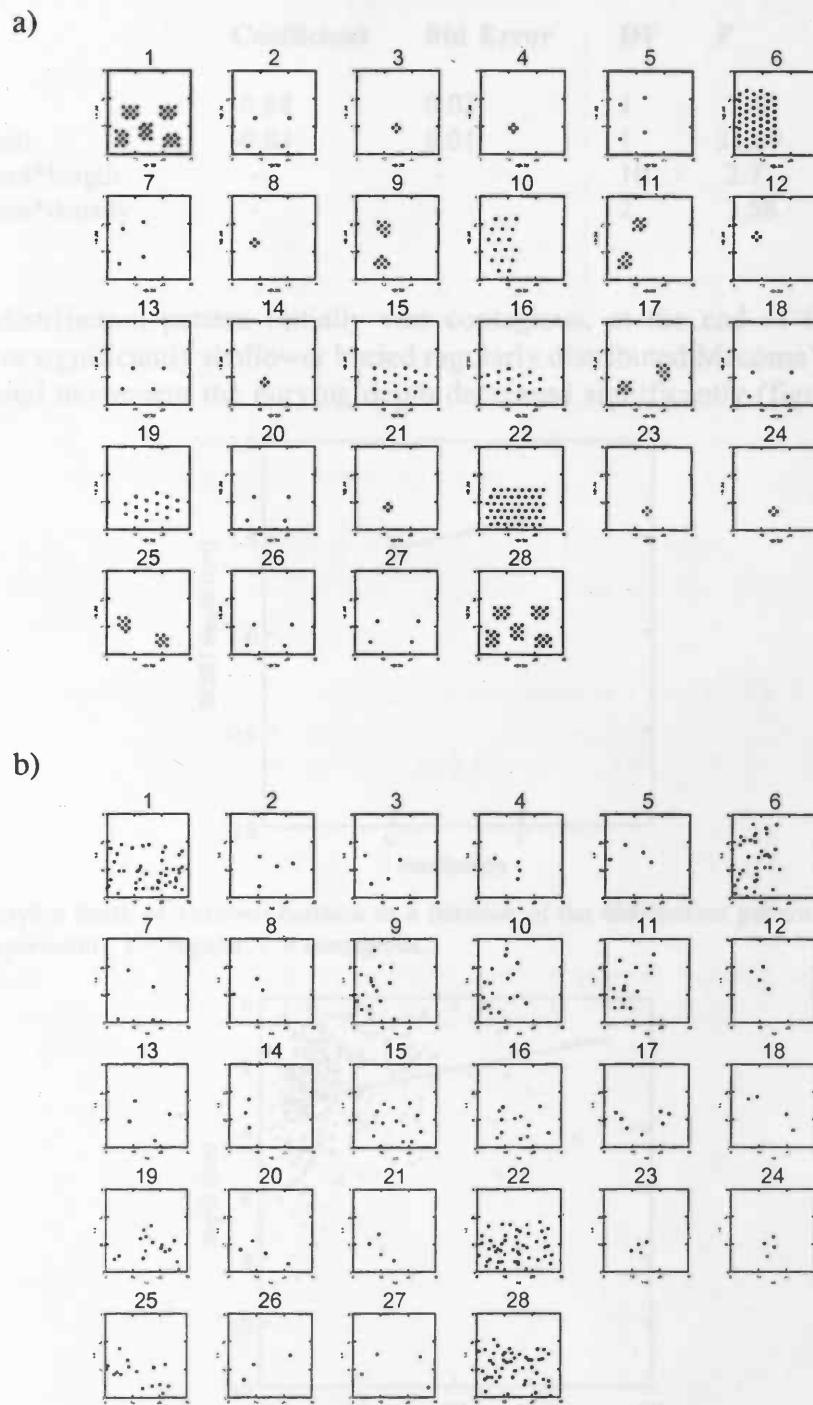
a)



b)



Figure 21. The spatial distribution of *Macoma balthica* at the start; a) and at the end of experiment IBN; b).

The effect of density on square root transformed burying depth (vertical distribution) was analysed with a stepwise GLM. Further factors were; distribution pattern (at start of experiment), total movement (horizontal distribution during the experiment), length and the relevant interactions between these four factors (table 5).

Table 5. Stepwise GLM of the dependent variable burying depth; n = 341; $R^2$ = 0.17.

| Factor | Coefficient | Std Error | DF | F | 'p' |
|---|---|---|---|---|---|
| distribution | -0.08 | 0.03 | 1 | 7.46 | 0.01 |
| total movement | -0.03 | 0.01 | 1 | 21.69 | 0.00 |
| total movement*length | - | - | 10 | 2.77 | 0.00 |
| total movement*density | - | - | 2 | 3.58 | 0.03 |

Where the distribution pattern initially was contagious, at the end of the experiment the Macoma were significantly shallower buried regularly distributed Macoma's (figure 22). With increasing total movement the burying depth decreased significantly (figure 23).
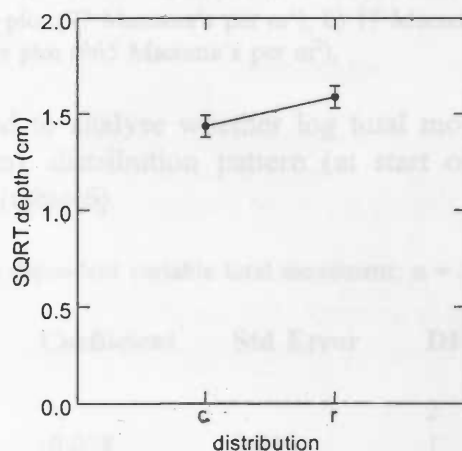


Figure 22. Burying depth of *Macoma balthica* as a function of the distribution pattern (at the start of the experiment); r = regular; c = contagious.
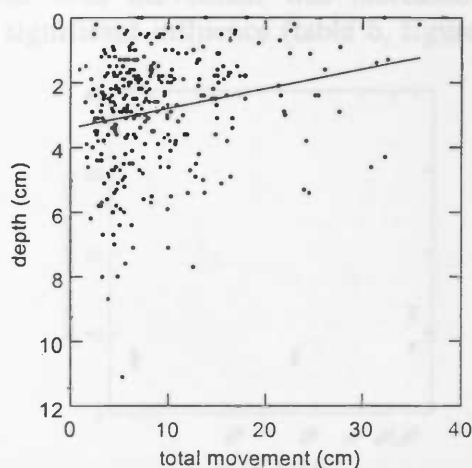


Figure 23. Burying depth of *Macoma balthica* as a function of the total movement.

23

The interactions total movement * length and total movement * density had significant influences. Figure 24 shows that with increasing density the slope of the regression line of depth * total movement decreased significantly.
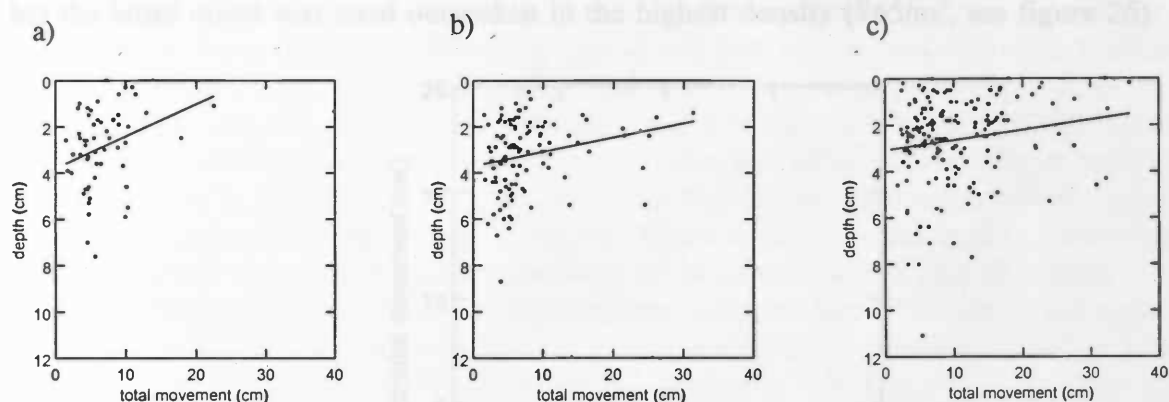
a)                          b)                          c)



Figure 24.  Burying depth of *Macoma balthica* as a function of the total movement for each density;
a) 4 Macoma's per plot (77 Macoma's per m$^2$); b) 17 Macoma's per plot (328 Macoma's per m$^2$)
c) 50 Macoma's per plot (965 Macoma's per m$^2$).

A stepwise GLM was used to analyse whether log total movement is changed by density, depth (vertical distribution), distribution pattern (at start of the experiment), length and their relevant interactions (table 6).

Table 6.  Stepwise GLM of the dependent variable total movement; n = 340; R$^2$ = 0.16.

| Factor | Coefficient | Std Error | DF | F | 'P' |
|---|---|---|---|---|---|
| density | . | . | 2 | 11.01 | 0.000 |
| burying depth | -0.078 | 0.019 | 1 | 17.01 | 0.000 |
| density*distribution | . | . | 2 | 10.63 | 0.000 |

With increasing density the total movement was increased significantly (table 6), also distribution patterns had a significant influence (table 6, figure 25).
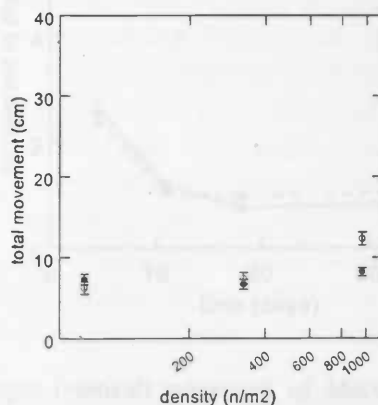


Figure 25.  Total movement of *Macoma balthica* as a function of densities of two different distribution patterns (at the start of the experiment); ○ = regular, ● = contagious.

24

Corresponding with the depth analysis a significant decrease in total movement was shown with increasing depth (table 6, figure 23).

The horizontal movement decreases over time during the first three measurements and at the end (fourth sampling point) there was an increase, all densities showing the same trend but the latter effect was most outspoken in the highest density (965/m², see figure 26).
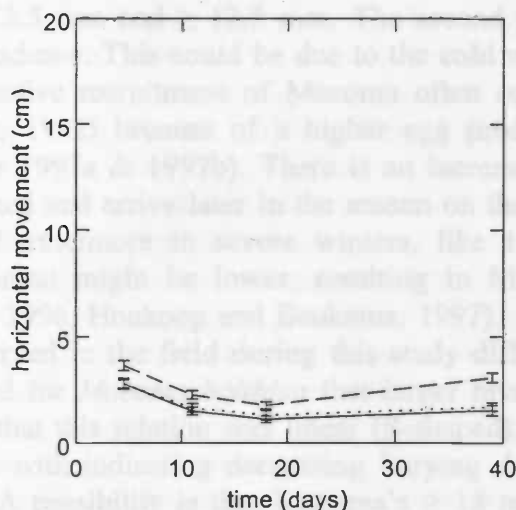


Figure 26.  Variation in time of horizontal movement of *Macoma balthica* for three different densities; (___) 4 Macoma's per plot (77 Macoma's per m²); (. . .) 17 Macoma's per plot (328 Macoma's per m²); (---) 50 Macoma's per plot (965 Macoma's per m²).

The same trend was seen in the depth movement over time with differences between densities but in distribution patterns (figure 27). Regular distributed Macoma's were buried deeper as contagious distributed Macoma's (compare table 5).
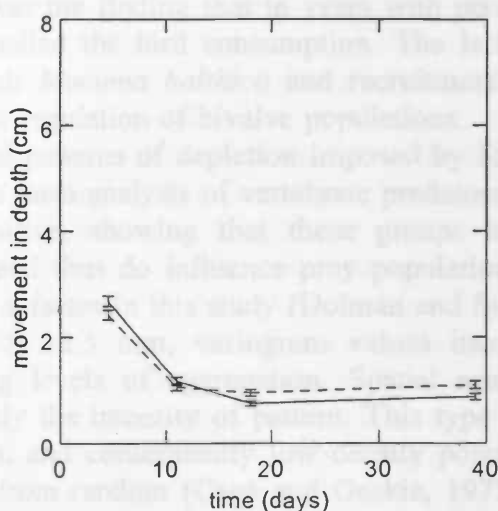


Figure 27.   Variation in time of depth (vertical) movement of *Macoma balthica* for two different distribu tions; regular (---); contagious (___).

# DISCUSSION

The Population of *Macoma balthica* studied here exhibits a bimodal size class-distribution. This type of distribution is common in marine molluscs which grow more slowly as they get older (Brown and Seed, 1977). This typical bimodal size class-distribution facilitates a division in length-class < 12.5 mm and ≥ 12.5 mm. The second year length-class (< 12.5 mm) showed a marked abundance. This could be due to the cold winter 1995/1996, since it has been observed that massive recruitment of Macoma often occurs after a cold winter (Beukema, 1982; Beukema, 1992) because of a higher egg production (Beukema, 1992; Honkoop and van der Meer 1997a & 1997b). There is an increased survival since benthic predators are severely reduced and arrive later in the season on the tidal flats after a severe winter (Beukema, 1992). Furthermore in severe winters, like 1996/1997, the metabolic costs in relation to food input might be lower, resulting in Macoma's having a better condition in spring (Zwarts 1996; Honkoop and Beukema, 1997).

The depth distribution observed in the field during this study differed from the one found by Zwarts (1996). He found for *Macoma balthica* that larger bivalves lived deeper buried than the smaller ones, and that this relation was linear (S-shaped). In this study a more U-shaped relation was found, with indicating decreasing burying depth with increasing size for lengths above 18 mm. A possibility is that Macoma's > 18 mm are less vulnerable to predators. The main predator of large Macoma's is the Oystercatcher. Ample indirect evidence exists indicating that Oystercatchers ignore Macoma's living at 4 to 6 cm depth, because these prey, although still accessible, are unprofitable due to the increase in handling time with burying depth. Therefore, Macoma's are relatively safe from bird predation when living 4 or 5 cm beneath the surface of the sediment (Zwarts, 1996). Macoma's larger than 18 mm are not an interesting prey for Knots, the overall main predator of *Macoma balthica*.

Van der Meer found that *Macoma balthica* has an annual mortality of around 40%. Bird consumption and bivalve elimination of the suitable part of the population were found to be unrelated. More curious was the finding that in years with poor bivalve stocks, bivalve elimination more or less equalled the bird consumption. The lack of a clear relationship between the numbers of adult *Macoma balthica* and recruitment indicates that predation has only a minor influence on regulation of bivalve populations.

In contrast, a study on spatial patterns of depletion imposed by foraging vertebrates found that the mean correlation in a meta-analysis of vertebrate predators of invertebrate prey (22 cases) was significantly positive, showing that these groups tend to impose spatially density-dependent depletion and thus do influence prey population structure. Depth distribution was not considered as a factor in this study (Dolman and Sutherland, 1997).

In the grid for lengthclass ≥ 12.5 mm, variogram values increased significantly with distance indicating increasing levels of aggregation. Spatial analysis based on variance estimates indicates at best only the intensity of pattern. This type of analysis is influenced by the number of individuals, and consequently low density populations are less likely to show significant differences from random (Cage and Geekie, 1973). It is possible that the length class < 12.5 mm, which showed a random distribution, had a low density which was to low for a powerful analysis.

The variance and mean density plot indicated two different distribution patterns in accordance with variogram results; contagious distribution for length class ≥ 12.5 mm and random distribution for lengthclass < 12.5 mm.

The dispersion index ($I_d$) showed no significant trend with increasing distance, in contrast to variogram results. $I_d$ of several sites showed significant, contagious distributions for length class $\geq$ 12.5 mm. No significance was found for a uniform distribution, but at several sites length class < 12.5 mm showed a slight tendency towards a uniform spatial pattern. A remarkable finding was that in area A4 with an $I_d$ of 1.4 for lengthclass $\geq$ 12.5 mm the spatial pattern was not significantly different from random. This could indicate that the number of cores sampled is too low to determine significant results.

Most studies found the aggregated pattern being most common in benthic populations. However whether or not a population is called contagious may depend on the index used. The most commonly used index to describe spatial patterns is the variance/mean ratio. The strong density dependence of this index is quite disadvantageous because comparisons of aggregation patterns is only possible at the same density level (Meire *et el.*, 1989). Zwarts (1988) found in very aggregated prey population there was an increase in variance of the sample mean. More samples were necessary to ensure accuracy. Cassie (1963) noted that methods of sorting distributions into contagious, regular or random rely on the distribution of density estimates about the mean rather than the actual spatial arrangement of individuals. In general there are two main problems in measuring variability in space and time. The first problem is how to quantify variation when the mean and variance of the population are not independent. There is no simple and general method of standardising variance. Selection of the size of the spatial and/or temporal unit is the second main problem (Lepš, 1993).

Kosler (1968) concluded that aggregated patterns are characteristic for macrobenthos of the eulitoral zone. Only bivalves with a low density were random distributed. Holme (1950) found an uniform pattern for the bivalve *Tellina tenuis*. Commito (1982) studied the spatial distribution of 0-year class and older *Mya arenaria* and *Macoma balthica* from the sandy mud flats in Cobscook Bay (USA) using a dispersion index, Morisita's index. First year individuals of both species had significantly aggregated spatial distributions. Although older *Mya arenaria* were usually aggregated, the older *Macoma balthica* were randomly distributed and showed a slight tendency towards an uniform spatial pattern. Zwarts' study (1988) with $I_d$ determination showed that first-year class *Mya arenaria* exhibit very aggregated distribution patterns, whereas older *Mya arenaria* were randomly distributed. The distribution pattern of the first-year-group of *Macoma balthica* resembled that of the older group rather than that of the spat in a study by Beukema (1993). Within the current study Macoma's $\geq$ 12.5 mm ( 2-years class and older) were found to exhibit a contagious distribution on a scale of 6 to 1100 metre radius. This in contrast to Macoma's < 12.5 mm (first-year class and younger), which showed a random distribution with a slight tendency towards an uniform distribution. The difference in distribution between the two length classes might attributed to the strategy of timely shifts during the first year of their live. Furthermore Piersma (1994) found that *Macoma balthica* in the Wadden Sea showed marked spatial and between-year variation in their distribution and abundance. Comparing the current study with previous studies reveals varying conclusions about spatial distribution between year classes of *Mya arenaria* and *Macoma balthica*. All studies use more or less different indexes and also sample size and scale vary, leaving similarities or differences between results unclear. Furthermore the differences might be due to the abiotic conditions at the sampling sites. McLusky and Elliot (1981), Newell (1965), Ankar (1977) and Tunnicliffe and Risk (1977) found a correlation between the density of *Macoma balthica* and the proportion of silt and clay in the sediments. However no overall correlation between the density and sediment particle size was found. These findings suggest that a strategy of

selecting finer substrate by Macoma is of value to this predominantly deposit feeder since such substrate supports a richer microflora. Also Martini and Morrison (1987) found for *Macoma balthica* highly correlated frequencies of occurrence with fine to very fine sand and silt. In a study of density dependence in suspension-feeding and deposit-feeding populations of *Macoma balthica* in field experiments was shown that growth of clams was density dependent in the muddy sand sediment (deposit feeding), but no such effect could be demonstrated for clams in the sandy sediment. Macoma filter feeds when suspended food material is abundant and begins deposit feeding as food supply decreases (Olafsson, 1986). Since it is not proven which kind of foraging *Macoma balthica* prefer, this bivalve is considered a facultative suspension/deposit feeder within this study.

The current study showed differences in density between dry and wet microhabitat sampling within the largest scale of the grid. There was a trend that density in dry habitat was higher than in the wet habitat. The lower density in wet habitat cores could be due to predation by Knots, since Knots might prefer to search for food in wet sediment. Alternatively Macoma had migrated to dry sediment in influence of Knot predation/presence.

Analysis of changes in spatial distribution along environmental gradients or during periods of recruitment would be very useful in extending our understanding of ecological processes and responses to environmental stress.

The zones exhibiting heterogeneity occur as populations undergo spatial structuring through processes as reproduction, death, predator-prey interactions, food availability, parasitism and so on (Allen and Star, 1982).

Experiments at individual level for lengthclass $\geq 12.5$ mm were useful in studying whether density or other factors like length, siphonweight, parasitism influenced depth and spatial distribution. Experiments on Richel showed only minor migration and hardly any predation by other predators than waders, the latter being excluded from the experiments. Here crabs were found to predate on Macoma's of large sizes, above 20 mm. This indicates that larger Macoma's do have other predators even when their size is to large for Knots. It is possible that the death of the four Macoma's were caused by a shallow burying depth or a slower burying rate, caused by a higher level of interaction between the individual Macoma's (three of four Macoma's were from plots with the highest densities).

The Richel field experiment data showed a similar pattern in depth distribution as the field data, indicating both representative experimental conditions and that 2 days sufficed for comparable burying depths. The depth distributions of the Richel field experiment could be explained by: length (negatively correlated), $AFDM_{siphon}$ (positively correlated), $DM_{shell}$ (negatively correlated), $AFDM_{meat}$ (only as an interaction factor) and density ($R^2 = 0.485$). Parasitism nor sex significantly explained the variance in depth. Other studies Kamermans (1992), Piersma (1994) and Zwarts (1996) found these relationships for depth distribution These studies ignored the factor density, which did not show a linear trend in this study, but was of indirect importance within the model used here. This might be due to two or more depth dependent factors affecting depth like predationrisk and foodsupply.

Depth distribution of *Macoma balthica* at the IBN experiment could be described using distribution pattern (at the start of the experiment), total movement and length and density as interaction factors. Future analysis of this data could include siphon length (as a limiting factor in burying depth), $DM_{shell}$ and $AFDM_{meat}$ of frozen individuals.

Horizontal distribution at the IBN experiment could be described using the factors density, depth and distribution pattern (at the start of the experiment), the latter being an interaction factor. Again, future analysis of the data could include siphon length, $DM_{shell}$, and $AFDM_{meat}$, of frozen individuals should also be taken in consideration.

28

Total horizontal movement and depth negatively correlated with each other. Highest rates of movement (both horizontal an vertical) were observed at the start of the experiment, suggesting an active effort of Macoma's in optimising their surroundings.

This hypothesis might also explain the increasing horizontal movement with increasing density. Regular distributed Macoma's were buried deeper than contagious distributed Macoma's. Intraspecific competition for food might be increasing since contagious distributed Macoma's are more tight packed. When food supply decreases a shallow burying depth is preferred (Olafsson, 1986). This reduction of the burying depth due to food supply may increase its value as prey and the risk to be predated. Whether or not Macoma's are aware of their predators , the interaction between Macoma and their predators might ultimately influence the depth distribution observed in the field.

Kamermans (1992) found that Macoma growth decreased with density, indicating intraspecific competition in *Macoma balthica* population, but not in *Cerastoderma edule* (suspensionfeeder). Interspecific competition did not occur between the two species. These results supported the hypothesis of Levinton (1972) that on a local scale, competition is expected more readily in deposit-feeding communities than in suspension feeding communities. The study of Olafsson (1986) also supported this hypothesis. Experiment IBN was conducted within the growth season of the shell (Zwarts, 1996), so the experiment may be expanded by remeasuring the length of the frozen Macoma's and comparing these data with determined lengths at the start of the experiment. Assuming sufficient growth, this method may reveal a relationship between growth and density. This study assessed more horizontal movement at higher densities. Moving demands energy, which than is unavailable for growth. Comparable considerations apply to depth movements and distribution patterns, as the finding of a relative increased vertical movement in regular distribution patterns opposite to contagious patterns within this study illustrates.

Further study of the distribution pattern on different smaller scales is possible with the data of experiment IBN. Further analysis on the data assessed in experiment IBN will include the determination of distribution patterns exhibited by *Macoma balthica* on a relatively small scale, which than will be compared with patterns investigated in the field.

# TANKWURD

As earste woe ik Tanja en Minne betankje foar de noflike slieperij yn Harns, wêr de hiele reis begûn. Spesiaal foar it ferfier nei de hafen. Alle minsken fan'e Richel woe ik graach tankje foar de moaie tiid en it selskip op en om'e waadtoer. Alhoewol't ik wer gjin kloften mientsen sjoen ha. Fjirder bin ik de minsken fan de polysjeboat P 96 en de Navicula tankber dat se ús nei en fan de sânbank fart hawwe.

It gebrûk fan'e tijbakken fan it IBN, Texel, haw ik tige wurdeare, sûnder dat wie it lêste eksperimint oergien. Dan no de hiele list fan minsken fan it NIOZ, wa ik yn it besûnder betankje woe:

Marco foar syn stipe as grutste nonneslachter,

Mirjam foar ús fûleindige plakproduksje,

Brabra foar de bêste tiid oer de kop,

Marieke foar de withoefaak Potvis oarkonde,

Jan Drent foar de swiid Systat leargong,

Ciska en Jasper foar it oerlibjen op'e Skorren,

Pleuni, Bart, Alex, Elfriede en Corinthe foar de learsum redendiele,

Bernhard foar it lienen fan syn blaue wein,

Jan van Gils foar it meiriden nei myn pake en beppe,

Pieternella foar de 400 nûmerkes mei triedsjes der oan,

Katja foar my nei Easterein te bringen,

Jaap foar syn statistyk rie,

Theunis foar de Fryske petearen

en Petra troch wa dizze hiele ûndernimming ûntstean is.

Fjirder woe ik Jolanda út Easterein tankje foar de geselligens en it farske brea-iten, Cato foar de nea ferfelende liften nei Grins en de bewenners en gasten fan de Potvis (spesiaal oan Sander) yn it bysûnder wannear't om iten giet: Petra, Eveline, Martijn, Ingrid, Doris, Regina, Oscar, Lianke, Corinthe, Alex, Elfriede, Corinthe, Pleuni, Bart, Pim en as lêste Jelmer foar fjirders syn rie, selskip ensafuorthinne, foar sa'n skoft dat hja tocht dat we boaskje wien.

Pim woe ik dan lang om let tankje foar syn begelieding, oars wie der nea in non troch my bestudearre en wie der grif neat mei se bart. At dat no oan'e breakrapte op Richel lei …

Mar Pim hat al myn proefbisten opiten en lykwols ha ik ek in pear priuwn.

Nei al dat Ingelsk en Frysk woe ik Jan Dillingh tankje foar syn ferduldiche ûnderwiis yn myn taalflaters.

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